

University of Groningen

Zebra finch females prefer males with redder bills independent of song rate-a meta-analysis

Simons, Mirre J.P.; Verhulst, Simon

Published in:
 Behavioral Ecology

DOI:
[10.1093/beheco/arr043](https://doi.org/10.1093/beheco/arr043)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 2011

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Simons, M. J. P., & Verhulst, S. (2011). Zebra finch females prefer males with redder bills independent of song rate-a meta-analysis. *Behavioral Ecology*, 22(4), 755-762. <https://doi.org/10.1093/beheco/arr043>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Original Article

Zebra finch females prefer males with redder bills independent of song rate—a meta-analysis

Mirre J.P. Simons and Simon Verhulst

Behavioural Biology, Center for Life Sciences, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

Male zebra finches display multiple secondary sexual traits such as song and red bill coloration. This color is dependent on carotenoids, which enhance immune function and are antioxidants. A red bill may thus function as an indicator signal. The zebra finch is extensively used in the study of carotenoid-dependent signaling. However, studies of female mate preferences for redder bills show mixed results. Here, we report a meta-analysis of mate-choice studies that reveals that female zebra finches do prefer males with redder bills ($r = 0.61$), except when there was reduced opportunity for imprinting or when bill color was experimentally manipulated, which both reduced preference for red bills to approximately zero. The latter may either be due to aspects of the experimental design or due to bill color being correlated with another trait such as song rate as was previously suggested. We show, however, in a separate meta-analysis on a different set of studies that the correlation between bill coloration and song rate ($r = 0.14$) was significantly lower than the $r = 0.61$ between bill color and attractiveness. We conclude, therefore, that the role of bill coloration in mate choice cannot be solely due to an association with song rate. Thus, we conclude that females do prefer males with redder bills when there was sufficient opportunity for sexual imprinting, but to what extent this is causally related to the bill color remains to be established. **Key words:** bill coloration, mate choice, sexual coloration, sexual signaling, song rate, zebra finch. [*Behav Ecol* 22:755–762 (2011)]

INTRODUCTION

Zebra finches (*Taeniopygia guttata*) exhibit brightly red colored bills. Sexual traits often signal quality (Grafen 1990; Kotiaho 2001). In male zebra finches, reproductive success (Price and Burley 1994) and physiological indicators of quality such as immune functioning and condition are positively correlated with bill redness (Birkhead et al. 1998; Birkhead et al. 2006; Bolund et al. 2010). Experimentally, an immune challenge (Alonso-Alvarez et al. 2004; Gautier et al. 2008; Cote et al. 2010) and cold exposure (Eraud et al. 2007) have been shown to decrease zebra finch bill coloration. Male zebra finch bill coloration thus exhibits variation that reflects phenotypic quality with respect to physiological state.

The redness of sexual ornaments of many species, including the zebra finch's bill, is dependent on carotenoids (McGraw 2004; Olson and Owens 2005; Pike, Blount, Bjerkeng, et al. 2007). Carotenoids have multiple physiological functions, acting as antioxidants and supporting the immune system (Pérez-Rodríguez 2009) but cannot be synthesized by the animal itself and hence carotenoid availability is determined by the dietary intake. Because carotenoids may be limiting but physiologically important, carotenoid-dependent sexual ornaments may be particularly suitable as quality indicators, signaling immune functioning, and antioxidant capacity (Olson and Owens 1998). Recently, the role of carotenoids as antioxidants has been questioned (Costantini and Moller 2008). However, noncarotenoid antioxidants also increase carotenoid-dependent sexual coloration suggesting that carotenoid-dependent coloration does signal antioxidant capacity (Bertrand et al. 2006; Perez et al. 2008; Pike, Blount,

Lindström, and Metcalfe 2007). If carotenoid-dependent sexual traits do reliably signal antioxidant capacity (Hartley and Kennedy 2004; Pérez-Rodríguez 2009), mate choice for these traits may yield direct and/or indirect fitness benefits, explaining why such traits feature in mate selection.

Given that zebra finch bill color is extensively used in the study of carotenoid-dependent sexual signaling and that it reflects phenotypic quality, it is surprising that female preferences for bill color show little consensus among studies (Collins and ten Cate 1996). Furthermore, it has been suggested that the importance of bill color in mate choice is minor and that instead females prefer high song rates (i.e., display rate), which covaries with bill color (Collins et al. 1994; Collins and ten Cate 1996), hence resulting in an apparent preference for redder bills in some studies.

Here, we combine all female mate-choice studies that we could find that presented the required information, using meta-analysis to test the hypothesis that female zebra finches prefer males with redder bills. Studies that correlate natural variation in male bill coloration with female choice cannot demonstrate causality because choosing females may rely on traits that covary with bill color resulting in a choice for redder bills. We therefore also included studies that manipulated bill color experimentally in our meta-analysis. We further tested whether the covariance between song rate and bill color can explain female choice for bill coloration as hypothesized by Collins and ten Cate (1996) by summarizing the correlation between song rate and bill coloration in a different set of studies.

MATERIALS AND METHODS

In a meta-analysis, the individual effect size estimates of different studies are weighted by study sample size to combine them into one average effect size. If this average effect size deviates significantly from zero, it can be concluded that overall the null hypothesis can be rejected, and hence this provides an objective synthesis of studies that tested a specific hypothesis.

Address correspondence to M.J.P. Simons. E-mail: m.j.p.simons@rug.nl.

Received 4 October 2010; revised 11 March 2011; accepted 12 March 2011.

© The Author 2011. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com

To test whether the correlation between attractiveness and bill color can be attributed to a correlation between bill color and song rate, our approach was to quantify the association between bill color and song rate using meta-analysis on a different set of studies and compare the strength of this correlation with the correlation between the color of a male's bill and his attractiveness. When the association between bill color and attractiveness is significantly stronger than the correlation between bill color and song rate we can infer that the association between bill color and attractiveness is not solely dependent on an association with song rate.

Female mate choice for male bill coloration

We searched studies using Google scholar and “zebra finch,” “female choice” or “female mate choice,” and “bill” or “beak” color (colour) as search terms and also checked the references of the retrieved papers for relevant material. Authors were contacted for relevant statistics not reported in papers. When studies did not report raw proportions of choice or test statistics or the raw data could not be measured from graphs or we did not succeed in contacting the authors, they could not be used (Immelmann 1959; Weisman et al. 1994).

The statistical approach between studies differed, with some reporting the preference for the reddest male and others reporting the relationship between the difference in redness and the resulting female preference. The second approach includes both the effect of the difference between males in redness together with the overall preference for the reddest male. We recommend reporting both in future research to ease comparison between studies. For the purpose of this review, we included both approaches because the rejection of either approach would have resulted in a substantial loss of studies. We preferred the statistic of the preference for the reddest males if both approaches were available.

Our own unpublished data were included in the meta-analysis. A classic 2-way choice trial was conducted in our outside aviaries (Haren, The Netherlands) for 2 h in between which males that could hear but not see each other were switched sides to control for side preferences. Preference was scored as time spent by the female at the side of the aviary of the male relative to the total time spent with either of the 2 males. Bill color was measured by the use of digital photography under controlled camera settings and lighting conditions (Simons MJP, in preparation). The redness of the bill was expressed as hue in HSV (Hue, Saturation, Value) color space.

A key element of meta-analysis is the selection of studies to include and unfortunately we had to omit the study by Roberts et al. 2007 on methodological grounds because the authors used principal component analysis to analyze spectrophotometric data of bills, which is difficult to compare with the methods applied by the other studies. The methods employed by the other studies were the Munsell method, photography, or photospectrometry, which were all expressed as hue. In the Munsell method, brightness (as well as saturation) is weighted but little in comparison with hue (Burley and Coopersmith 1987). Roberts et al. 2007 found that males with brighter bills (the principal component corresponding to brightness) were preferred by females; this finding can therefore not be interpreted as either positive or negative but rather as an incentive for further research on which aspects of the light reflected by zebra finch bills are found to be attractive.

Experimental studies

Some studies manipulated bill color using nail polish, polymer paint, or marker pen of wild-type or white morph birds

(Burley and Coopersmith 1987; Collins et al. 1994; Sullivan 1994; Vos 1995). To evaluate the effect of such manipulations, we used a moderator for studies that interfered with the natural appearance of males.

Sexual imprinting

In birds sexual imprinting, which can shape mating preferences, seems to be the rule rather than the exception (ten Cate and Vos 1999). In zebra finches, this process continues at least up to 46 days of age (which is the median period of imprinting experimentally shown to be still effective in shaping preference: ten Cate 1987; Vos et al. 1993) and requires close interaction with adult conspecifics (ten Cate et al. 1984). Bill color specifically has been shown to be a trait zebra finches imprint strongly on, to the extent that experimental imprinting conditions can reverse mate preferences with respect to bill color (Weisman et al. 1994; Vos 1995). The average imprinting opportunity in this set of studies ranged from short, 30–40 days, to long, 48–100 days, and we used these imprinting opportunity ranges as a 2-level categorical moderator in the analysis. This dichotomization was based on the length of the imprinting process, which was evaluated experimentally (ten Cate 1987; Vos et al. 1993). We also report the estimator for a continuous fit, but in further analyses, we use dichotomization for 3 reasons. First, it is well known that there are critical phases for imprinting and hence sexual imprinting is not a linear process. Second, dichotomization allowed us to compare the overall effect size of relatively long-imprinted individuals with the song rate bill color correlation. Third, it allowed us to include studies where the information provided on the imprinting period was not provided in great detail (Table 1). Three studies isolated chicks from adults at 30–40 days (Balzer and Williams 1998; Blount et al. 2003; Forstmeier and Birkhead 2004), 4 other studies kept chicks with adults on which they could imprint for a period which was on average over 48 days (see Table 1). Of these 3 studies, only Forstmeier and Birkhead (2004) reported their imprinting conditions; housing conditions from Balzer and Williams (1998) and Blount et al. (2003) were obtained through correspondence with the authors.

Song rate, bill color correlation

Search terms in Google scholar included “zebra finch” and “song” or “display” and “bill” or “beak” color/colour. Authors of studies that measured both song rate and bill coloration, but did not report how they correlated, were contacted. We restricted our analysis to studies that measured song rate without other male competitors present because this confounds song rate with female choice and behavior of the male competitor (this was the reason to omit de Kogel and Prijs 1996). This resulted in a total of 6 studies. In this analysis, we included studies regardless of the age up to which juveniles could imprint on adults because we are not aware of indications that this affects either bill color or song rate.

Statistics

Reported statistics were converted into Pearson's r using standard formulas (Rosenthal 1994). Proportions were converted into a χ^2 statistic before conversion to r . Pearson's r 's were converted into Fisher's Z 's before analysis (Nakagawa and Cuthill 2007). The meta-analyses were performed with the Metafor package (Viechtbauer 2010) in R (R Development Core Team 2009) using random effects meta-analysis fitted

Table 1
Summary of studies reporting female choice for male bill coloration

Study	Sample size	Independent sample size (corrected for possible pseudoreplication)	Statistic reported	Effect size (r)	Moderating variable	Bill color measurement method and other remarks	Opportunity to imprint on adults
Burley and Coopersmith (1987)	14	4	12/14	0.87	Long imprinting	Munsell	Between 34 and 62 days
	24	5	$\chi^2 = 13.35$ df = 1	0.43	Long imprinting	Munsell	Between 34 and 62 days
de Kogel and Prijs (1996)	26	9	$t = 4.97$ df = 24	0.71	Long imprinting	Munsell	50 days
Unpublished from our lab	21	21	$t = 3.31$ df = 19	0.60	Long imprinting	Digital photography, hue in HSV color space	100 days
Houtman (1992)	24	24	$F = 10.95$ df = 1,22	0.58	Long imprinting	Munsell	Birds were obtained from commercial breeders and the precise rearing conditions were not specified, but we have no reason to assume that chicks were isolated from adults before 46 days of age since to our best knowledge, commercial breeding usually takes place in aviaries.
Roberts et al. (2007)	48	8	$\chi^2 = 7.28$ df = 1	0.55	Not useable, brightness is incomparable with Munsell system data	Principal component of spectrophotometry corresponding to brightness	62 days
Vos (1995)	19	5	$t = -0.30$ df = 17	-0.07	Artificial manipulation	Measured from Figure 1a, t -test of arc sine converted values against hypothesized mean	55 days
Sullivan (1994)	11	5	6/11	0.09	Artificial manipulation		49 days
Burley and Coopersmith (1987)	25	7	18/25	0.44	Artificial manipulation	Munsell	Between 34 and 62 days
Collins et al. (1994)	8	8	$t = -1.64$ df = 6	-0.56	Artificial manipulation		Not available
Blount et al. (2003)	10	10	$t = 0.74$ df = 8	0.25	Short imprinting	Data obtained from author. t -test of arc sine converted values against hypothesized mean, Color measurement comparable with Munsell with use of the Dulux Trade Colour Palette	40 days
Balzer and Williams (1998)	33	33	$Z = 0.18$ df = 31	0.03	Short imprinting	Munsell	30 days
Forstmeier and Birkhead (2004)	77	77	$F = 1.465$ df = 1,77	-0.14	Short imprinting	Munsell	35 days

HSV, Hue, Saturation, Value.

with restricted maximum likelihood. When multiple effect sizes were extracted from one study, we used the weighted average. Each study was weighted by independent sample size $n - 3$ (Cooper et al. 2009). The studies were examined for within study pseudoreplication, which occurs when stimulus sets of males or individual females are used repeatedly. The independent sample size is therefore the sample size that could be used without risking pseudoreplication. For example, if 20 females were tested with 5 stimulus sets of males, we used 5 as the independent sample size.

Publication bias was investigated using funnel plots. In a funnel plot, publication bias is revealed by an increase in absolute effect size with decreasing sample size. The significance of this relationship was tested using a rank test (Viechtbauer 2010).

When studies use different methodology or there are differences between study populations, this induces variability in "true" effect sizes. The resulting heterogeneity between studies can be evaluated using the Q test (Viechtbauer 2010). A significant heterogeneity indicates that there are likely to be moderating variables that explain the variability between studies.

The studies that allowed for short- and long-imprinting periods and the experimental studies were coded in one moderating variable with 3 levels. These were nonoverlapping categories because all (except one study that did not report this information) studies that manipulated bills experimentally allowed for a long-imprinting period. The estimates reported

are the deviation from the group of studies that allowed for a long-imprinting period.

RESULTS

Do females prefer males with the reddest bill?

A total of 11 independent mate-choice studies were obtained (Table 1, Figure 1). Our analysis revealed an average effect size of $r = 0.28$, (95% confidence interval [CI] 0.0006 – 0.52) showing that on average, females preferred males with redder bills ($z = 1.96$, $P < 0.05$). Heterogeneity was significant however ($Q = 26.4$, $P = 0.003$).

The moderator coding for imprinting conditions and experimental bill manipulation explained a significant proportion of this variance ($df = 2$, $Q = 21.93$, $P < 0.0001$). The average effect size of studies that allowed for a long-imprinting period ($n = 4$) turned out to be significantly higher than the average effect size of the studies ($n = 3$) with limited opportunity for imprinting (difference: -0.65 , $z = -4.59$, $P < 0.0001$) and also significantly higher than the average effect size of the experimental studies ($n = 4$; difference: -0.67 , $z = -2.58$, $P < 0.01$). Less opportunity for imprinting and artificial manipulation thus reduced female preference for red male bill coloration to approximately zero ($0.61 - 0.65$ or $0.67 = -0.04$ or -0.06). When imprinting opportunity (in days) was fitted as a continuous linear moderator (which reduced sample

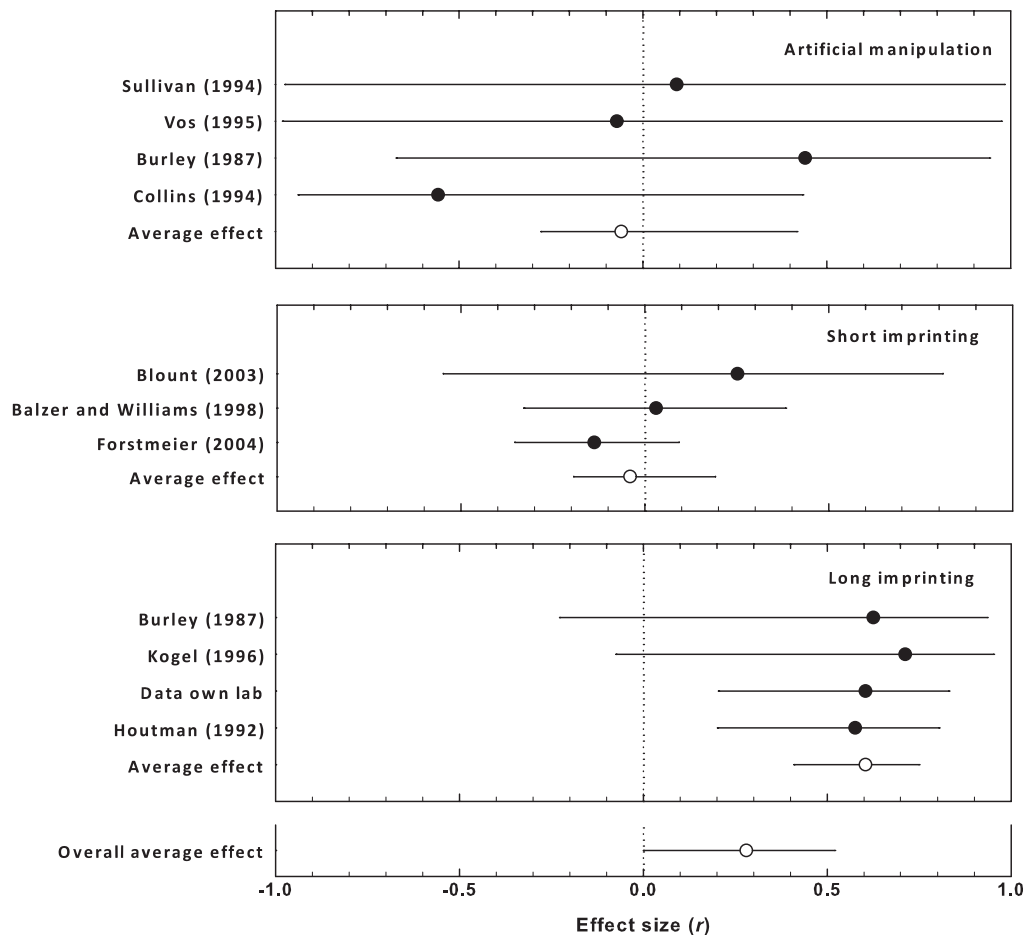


Figure 1

Effect size of female preference for red bills ($r \pm 95\%$ CI calculated using independent sample size), ordered within each panel with respect to sample size, with the lowest sample size at the top. Bottom effect size is the average.

Table 2**Summary of studies reporting the correlation between male bill coloration and song rate**

Study	Sample size	Statistic reported (effect size, r)	Bill color measurement method and other remarks
Birkhead and Fletcher (1995)	10	0.05	Munsell
Houtman (1992)	22	0.45	Munsell
Birkhead et al. (1998)	31	0.13	Munsell, measured and analyzed from their Figure 4
Unpublished from Barbara Tschirren	57	-0.25	Hue calculated from spectrophotometry, for methods see Pryke et al. (2001), Tschirren et al. (2009)
Bolund et al. (2010)	76	0.26	Munsell
Forstmeier and Birkhead (2004)	104	0.20	Munsell

size) this turned out to be also significantly correlated with preference for red bills ($n = 6$, $z = -1.98$, $P = 0.048$).

In nonexperimental studies where birds did have ample imprinting opportunity, the average effect size was $r = 0.61$ (95% CI 0.41–0.75; $z = 5.06$, $P < 0.001$) with nonsignificant heterogeneity ($Q = 0.26$, $P = 0.97$). The latter effect size, without the confounding effects of limited imprinting opportunity and bill color manipulation, we consider the best estimate of the strength of the relationship between male bill coloration and female mate choice. We used this effect size in the comparison with correlation between song rate and bill color.

Song rate and comparison with female mate-choice effect

We found 6 independent studies that reported the correlation between song rate and bill color (Table 2, Figure 2). The average effect size was $r = 0.14$, and the 95% CI included zero (-0.07 to 0.34 ; $z = 1.30$, $P = 0.19$). This suggests that the relationship between song rate and bill coloration of male zebra finches is weak on average and not significant. Heterogeneity was significant ($Q = 12.5$, $P = 0.03$).

When we compared this average effect ($r = 0.14$) with the average effect size of female mate choice for males with redder bills ($r = 0.61$), using a Student's t -test on the average effect sizes with their corresponding standard errors under the assumption of unequal variance, this revealed that the latter was significantly higher ($t = 3.23$, $P = 0.018$). Female choice for red bills can therefore not be solely dependent on the correlation between song rate and bill coloration (see MATERIALS AND METHODS).

Publication bias

Funnel plots (Figure 3) did not reveal a publication bias, but this is difficult to detect with this relatively limited sample of

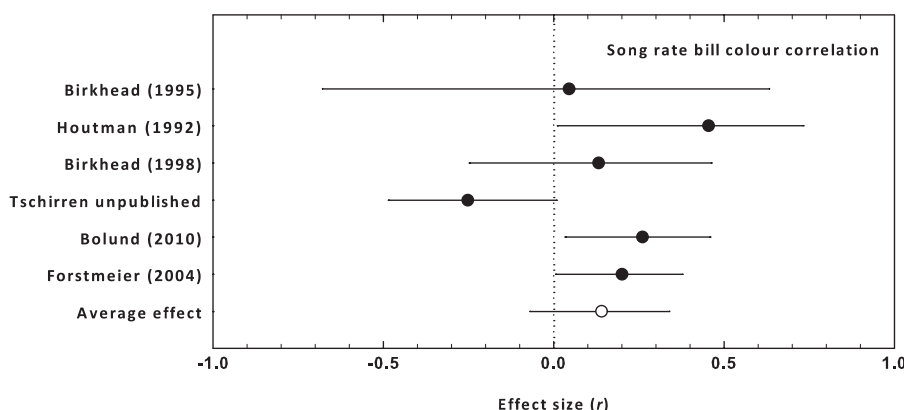
studies. Rank tests for funnel plot asymmetry were nonsignificant for both analyses (Kendall's tau > -0.09 , $P > 0.70$).

DISCUSSION

Red is preferred

Previous studies reported mixed results with respect to the role of male bill color in female mate choice in zebra finches. Using meta-analysis, we show that female zebra finches on average prefer males with redder bills, which is in agreement with the reported link between bill color and phenotypic quality (see INTRODUCTION). Given that bill coloration signals phenotypic quality, female choice for redder bills selects for males with higher phenotypic quality.

It has previously been suggested (Collins et al. 1994; Collins and ten Cate 1996) that observed mating preference for males with redder bills might be due to mate selection for song rate, when this is positively associated with bill redness. However, our meta-analysis revealed that the association between bill redness and song rate was not very strong ($r = 0.14$) and not significant and significantly lower than the reference effect size for preference for redder bills ($r = 0.61$). This implies that the latter effect cannot be fully explained by the correlation between male bill color and song rate. A large difference in measurement error between mate choice and song rate could, however, also be responsible for this difference because random measurement error reduces effect sizes. However, measurement error of mate choice is probably higher than that of song rate, given that mate choice is a behavioral trait with relatively low repeatability (Bell et al. 2009) whereas song rate has been reported to be highly repeatable (Birkhead and Fletcher 1995; Forstmeier and Birkhead 2004). Thus, we consider it unlikely that the difference between the 2 effect sizes is due to a difference in measurement error.

**Figure 2**

Effect size of ($r \pm 95\%$ CI) the song rate/ bill coloration relationship ordered from top to bottom with respect to sample size, starting with the lowest sample size. Bottom effect size is the average.

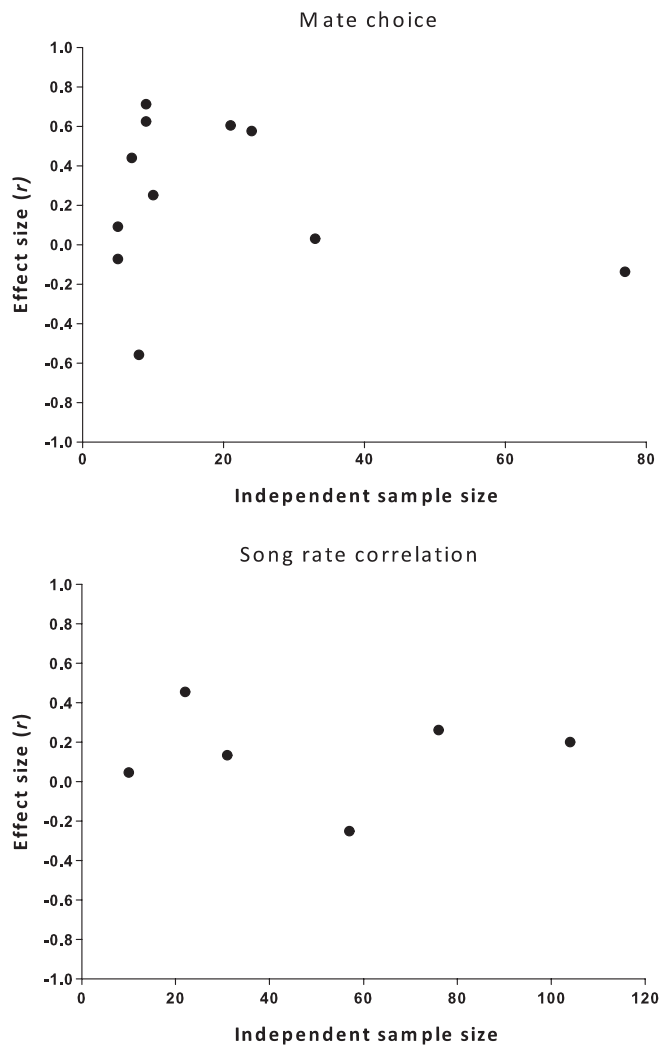


Figure 3
Funnel plots of both meta-analyses. Independent sample size is plotted against the effect size for each study.

The proportion of variance in female choice explained by male bill coloration is $0.61^2 = 0.37$. The proportion that cannot be due to the song rate/bill color correlation is $0.37 - 0.14^2 = 0.35$. This considerable amount of explained variance increases our confidence in the signaling function of the male zebra finch bill. However, it still leaves a considerable part of variance to be explained (0.65 if error is ignored). This means that other (sexual) traits have the potential to be more important in mate choice as bill coloration.

Due to the correlative nature of the mate choice studies the effect of bill color does not necessarily imply that females discriminate between potential mates using bill coloration. Instead, they may select on traits other than song rate that do covary with bill color. Possible candidates are song content (Holveck and Riebel 2007; Riebel 2009), UV reflectance (Bennett et al. 1996), and chest plumage symmetry (Swaddle and Cuthill 1994), which have all been shown to play a role in zebra finch mate choice. A way to establish to what extent bill color is causally involved in the strong preference for redder bills is to study the effect of manipulated bill color on attractiveness. However, the available experimental studies show no effect on average (Figure 1). There can be different reasons for the conspicuous contrast between the experimental and observational results, including of course, as discussed above,

that females base mate choice on other traits that show, however, a fairly strong correlation with bill color. Alternatively, there could be methodological aspects of the experimental studies that explain the negligible effect size, such as the challenge to manipulate bill color while maintaining a fully natural appearance of bill color. Furthermore, even when the manipulation is successful in maintaining the natural appearance of the bill, the manipulation may create a mismatch between bill color and other sexual signals, which in itself may change female perception of the male (e.g., Künzler and Bakker 2001). Lastly, different control groups are missing from the experimental studies, which makes these studies difficult to interpret and compare. When a female is presented with a male manipulated to be more attractive and an unmanipulated male (as in Burley and Coopersmith 1987), the lack of a sham-manipulated group limits the strict conclusion from such experiments to: female zebra finches prefer or do not prefer artificially manipulated males. When both males are manipulated (as in Collins et al. 1994 and Sullivan 1994), the resulting artificial signal might cause females to behave abnormally if it does not adequately mimic the natural signal (as also argued in Collins and ten Cate 1996). A design that includes nonmanipulated, sham-manipulated, and manipulated to be attractive or less attractive could increase our understanding of the causality of female choice for male red bill coloration. Hence, bill color manipulations can show a causal effect of bill color, but failing to reject the null hypothesis can be attributable to the general approach rather than to the absence of causality.

Imprinting

In zebra finches, mating preferences are at least partly shaped during imprinting at least up to 46 days of age (ten Cate 1987; Vos et al. 1993) and bill color specifically has been shown to be an important trait in this imprinting process (Weisman et al. 1994; Vos 1995). In agreement with these findings, reduced opportunity for imprinting after the age of 30–40 days resulted in an absence of preference for red male bill coloration. This effect may arise because the preference for red bill ornamentation was not fully imprinted, which could have resulted in reduced kin or sex recognition, which in its turn affected mate choice. Imprinting could have continued after 30–40 days in the groups in which juveniles were kept (personal information from authors) among which bill color had not developed its coloration from black to reddish (de Kogel 1997) resulting in a preference for juvenile coloration. Other aspects of the imprinting process other than specific imprinting on bill coloration can also be responsible for the differences we find. Reduced kin or sex recognition, which is the potential result from a short imprinting period, could affect mate-choice decisions in general resulting in no preference for bill coloration. Thus, our analysis confirms that husbandry practices can critically affect female choice with respect to bill color, as previously suggested (Forstmeier and Birkhead 2004) and also reported for song (Riebel 2000). Note, however, that the imprinting effect we report is based on a limited number of studies, and in our view, this result should above all be seen as a good reason to evaluate this pattern with an experiment. An effect of imprinting will be important in the interpretation of studies on sexual selection in the zebra finch, and we suggest it would be prudent to control and report imprinting conditions in detail in future studies.

Male choice

We have focused on female choice, but zebra finches form stable pair bonds with mutual mate choice (Silcox and Evans

1982; Monaghan et al. 1996). Hence, the evolution of bill color will also depend on male preferences, but unfortunately male choice for female bill color has been investigated in only 2 studies (Burley and Coopersmith 1987; de Kogel and Pijls 1996). Burley and Coopersmith (1987) reported a preference for orange females compared with red, but extreme orange toward yellowish females were avoided. de Kogel and Pijls (1996) reported a nonsignificant preference for females with more orange bills compared with red. Interestingly, females with more orange bills were found to have increased reproductive output and survival (Price and Burley 1994), suggesting males should prefer females with more orange bills compared with red. However, females with redder bills deposit more carotenoids into their eggs and increased yolk carotenoids are associated with increased hatching and fledging success (McGraw et al. 2005). Further study is required before conclusions can be reached regarding the association between female bill color and her sexual attractiveness, and hence the role of male mate choice in the evolution of bill color.

CONCLUSIONS

We found a significant overall preference for males with redder bills and we show that the overall effect is significantly higher than the correlation between song rate and bill coloration. This leads us to reject the hypothesis (Collins et al. 1994; Collins and ten Cate 1996) that the preference for red bill coloration is a result from this correlation. Additionally, the significant moderating effect of imprinting on female choice for bill coloration warrants experimental testing of this effect.

FUNDING

Netherlands Organization of Scientific Research (NWO) Top-talent grant to M.J.P.S. and an NWO Vici grant to S.V.

Egbert Koetsier and undergraduate students collected the mate-choice data in our laboratory. Jonathan Blount and Barbara Tschirren kindly provided unpublished data. Katharina Riebel alerted us to the importance of imprinting, and Wolfgang Forstmeier, Tony Williams, Tim Birkhead, and Jonathan Blount discussed their methodology with us. We thank Shinichi Nakagawa and Wolfgang Viechtbauer for advice for the meta-analysis. Carel ten Cate provided valuable comments on an earlier version of the manuscript.

REFERENCES

- Alonso-Alvarez C, Bertrand S, Devevey G, Gaillard M, Prost J, Faivre B, Sorci G. 2004. An experimental test of the dose-dependent effect of carotenoids and immune activation on sexual signals and antioxidant activity. *Am Nat*. 164:651–659.
- Balzer AL, Williams TD. 1998. Do female zebra finches vary primary reproductive effort in relation to mate attractiveness? *Behaviour*. 135: 297–309.
- Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. *Anim Behav*. 77:771–783.
- Bennett ATD, Cuthill IC, Partridge JC, Maier EJ. 1996. Ultraviolet vision and mate choice in zebra finches. *Nature*. 380:433–435.
- Bertrand S, Faivre B, Sorci G. 2006. Do carotenoid-based sexual traits signal the availability of non-pigmentary antioxidants? *J Exp Biol*. 209:4414–4419.
- Birkhead TR, Fletcher F. 1995. Male phenotype and ejaculate quality in the zebra finch *Taeniopygia guttata*. *Proc R Soc B Biol Sci*. 262: 329–334.
- Birkhead TR, Fletcher F, Pellatt EJ. 1998. Sexual selection in the zebra finch *Taeniopygia guttata*: condition, sex traits and immune capacity. *Behav Ecol Sociobiol*. 44:179–191.
- Birkhead TR, Pellatt EJ, Matthews IM, Roddis NJ, Hunter FM, McPhie F, Castillo-Juarez H. 2006. Genic capture and the genetic basis of sexually selected traits in the zebra finch. *Evolution*. 60: 2389–2398.
- Blount JD, Metcalfe NB, Birkhead TR, Surai PF. 2003. Carotenoid modulation of immune function and sexual attractiveness in zebra finches. *Science*. 300:125–127.
- Bolund E, Martin K, Kempenaers B, Forstmeier W. 2010. Inbreeding depression of sexually selected traits and attractiveness in the zebra finch. *Anim Behav*. 79:947–955.
- Burley NT, Coopersmith C. 1987. Bill color preferences of zebra finches. *Ethology*. 76:133–151.
- ten Cate C. 1987. Sexual preferences in zebra finch males raised by two species: II. The internal representation resulting from double imprinting. *Anim Behav*. 35:321–330.
- ten Cate C, Los L, Schilperoord L. 1984. The influence of differences in social experience on the development of species recognition in zebra finch males. *Anim Behav*. 32:852–860.
- ten Cate C, Vos D. 1999. Sexual imprinting and evolutionary processes in birds: a reassessment. *Adv Study Behav*. 28:1–31.
- Collins SA, ten Cate C. 1996. Does beak colour affect female preference in zebra finches? *Anim Behav*. 52:105–112.
- Collins SA, Hubbard C, Houtman AM. 1994. Female mate choice in the zebra finch—the effect of male beak colour and male song. *Behav Ecol Sociobiol*. 35:21–25.
- Cooper HM, Hedges LV, Valentine JC. 2009. The handbook of research synthesis and meta-analysis. 2nd ed. New York: Russell Sage Foundation.
- Costantini D, Moller A. 2008. Carotenoids are minor antioxidants for birds. *Funct Ecol*. 22:367.
- Cote J, Arnoux E, Sorci G, Gaillard M, Faivre B. 2010. Age-dependent allocation of carotenoids to coloration versus antioxidant defences. *J Exp Biol*. 213:271–277.
- Eraud C, Devevey G, Gaillard M, Prost J, Sorci G, Faivre B. 2007. Environmental stress affects the expression of a carotenoid-based sexual trait in male zebra finches. *J Exp Biol*. 210:3571–3578.
- Forstmeier W, Birkhead TR. 2004. Repeatability of mate choice in the zebra finch: consistency within and between females. *Anim Behav*. 68:1017–1028.
- Gautier P, Barroca M, Bertrand S, Eraud C. 2008. The presence of females modulates the expression of a carotenoid-based sexual signal. *Behav Ecol Sociobiol*. 62:1159–1166.
- Grafen A. 1990. Biological signals as handicaps. *J Theor Biol*. 144: 517–546.
- Hartley RC, Kennedy MW. 2004. Are carotenoids a red herring in sexual display? *Trends Ecol Evol*. 19:353–354.
- Holveck MJ, Riebel K. 2007. Preferred songs predict preferred males: consistency and repeatability of zebra finch females across three test contexts. *Anim Behav*. 74:297–309.
- Houtman AM. 1992. Female zebra finches choose extra-pair copulations with genetically attractive males. *Proc R Soc B Biol Sci*. 249:3–6.
- Immelmann K. 1959. Experimentelle Untersuchungen über die biologische Bedeutung artspezifischer Merkmale beim Zebrafinken (*Taeniopygia castanotis* Gould). *Zool Jahrb Abt Syst Ökol Geogr Tiere*. 86:437–592.
- de Kogel CH. 1997. Long-term effects of brood size manipulation on morphological development and sex-specific mortality of offspring. *J Anim Ecol*. 66:167–178.
- de Kogel CH, Pijls HJ. 1996. Effects of brood size manipulations on sexual attractiveness of offspring in the zebra finch. *Anim Behav*. 51: 699–708.
- Kotiaho JS. 2001. Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biol Rev*. 76:365–376.
- Künzler R, Bakker T. 2001. Female preferences for single and combined traits in computer animated stickleback males. *Behav Ecol*. 12:681–685.
- McGraw K, Adkins-Regan E, Parker R. 2005. Maternally derived carotenoid pigments affect offspring survival, sex ratio, and sexual attractiveness in a colorful songbird. *Naturwissenschaften*. 92: 375–380.
- McGraw KJ. 2004. Colorful songbirds metabolize carotenoids at the integument. *J Avian Biol*. 35:471–476.
- Monaghan P, Metcalfe NB, Houston DC. 1996. Male finches selectively pair with fecund females. *Proc Biol Sci*. 263:1183–1186.
- Nakagawa S, Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol Rev Camb Philos Soc*. 82:591–605.

- Olson V, Owens I. 1998. Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol Evol.* 13:510–514.
- Olson VA, Owens IPF. 2005. Interspecific variation in the use of carotenoid-based coloration in birds: diet, life history and phylogeny. *J Evol Biol.* 18:1534–1546.
- Perez C, Lores M, Velando A. 2008. Availability of nonpigmentary antioxidant affects red coloration in gulls. *Behav Ecol.* 19:967–973.
- Pérez-Rodríguez L. 2009. Carotenoids in evolutionary ecology: re-evaluating the antioxidant role. *BioEssays.* 31:1116–1126.
- Pike TW, Blount JD, Bjerkeng B, Lindström J, Metcalfe NB. 2007. Carotenoids, oxidative stress and female mating preference for longer lived males. *Proc R Soc B Biol Sci.* 274:1591–1596.
- Pike TW, Blount JD, Lindström J, Metcalfe NB. 2007. Availability of non-carotenoid antioxidants affects the expression of a carotenoid-based sexual ornament. *Biol Lett.* 3:353–356.
- Price DK, Burley NT. 1994. Constraints on the evolution of attractive traits: selection in male and female zebra finches. *Am Nat.* 144:908–934.
- Pryke SR, Andersson S, Lawes MJ. 2001. Sexual selection of multiple handicaps in the red-collared widowbird: female choice of tail length but not carotenoid display. *Evolution.* 55:1452–1463.
- R Development Core Team. 2009. A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Riebel K. 2000. Early exposure leads to repeatable preferences for male song in female zebra finches. *Proc R Soc B Biol Sci.* 267:2553–2558.
- Riebel K. 2009. Song and female mate choice in zebra finches: a review. *Adv Study Behav.* 40:197–238.
- Roberts ML, Buchanan KL, Bennett ATD, Evans MR. 2007. Mate choice in zebra finches: does corticosterone play a role? *Anim Behav.* 74:921–929.
- Rosenthal R. 1994. Parametric measures of effect size. In: Cooper H, Hedges L, editors. *The handbook of research synthesis.* New York: Russell Sage Foundation Publications. p. 231–244.
- Silcox AP, Evans SM. 1982. Factors affecting the formation and maintenance of pair bonds in the zebra finch, *Taeniopygia guttata*. *Anim Behav.* 30:1237–1243.
- Sullivan M. 1994. Discrimination among males by female zebra finches based on past as well as well as current phenotype. *Ethology.* 96:97–104.
- Swaddle J, Cuthill I. 1994. Female zebra finches prefer males with symmetric chest plumage. *Proc R Soc B Biol Sci.* 258:267–271.
- Tschirren B, Rutstein AN, Postma E, Mariette M, Griffith SC. 2009. Short- and long-term consequences of early developmental conditions: a case study on wild and domesticated zebra finches. *J Evol Biol.* 22:387–395.
- Viechtbauer W. 2010. Conducting meta-analyses in R with the metafor package. *J Stat Software.* 36:1–48.
- Vos DR. 1995. The role of sexual imprinting for sex recognition in zebra finches: a difference between males and females. *Anim Behav.* 50:645–653.
- Vos DR, Prijs J, ten Cate C. 1993. Sexual imprinting in zebra finch males: a differential effect of successive and simultaneous experience with two colour morphs. *Behaviour.* 126:137–154.
- Weisman R, Shackleton S, Ratcliffe L, Weary D, Boag P. 1994. Sexual preferences of female zebra finches: imprinting on beak colour. *Behaviour.* 128:15–24.